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PECULIAR STAGES OF FOLIAGE IN THE GENUS ACACIA.

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THE development of foliage leaves in general appears, from the results of investigations made thus far, to be a regular increase in complexity, almost the same for the ontogeny of a single plant as for the race in historic development, as disclosed by fossil remains. As an especially good example may be mentioned a series given by Jackson ('99) illustrative of the history, both phylogenetic and ontogenetic, of *Liriodendron*. For the genus *Acacia*, Reinke ('96) gives a very comprehensive review of the development based upon the seedling forms and comparative study of the adults of the several subgenera, noting especially the phyllode-forming tendency.

As the first point which this paper aims to bring out deals with the bipinnate leaf and its development regardless of the phyllode, it may be well to call to mind the regular course of seedling leaf forms. The first leaf, after the cotyledons, is normally singly pinnate, with about four pairs of leaflets; the next is generally bipinnate, with but a single pair of pinnae; further change is a mere addition of more such pairs along the main axis. A peculiar transition stage between the singly pinnate and the bipinnate is sometimes found in seedlings of *A. leprosa* Sieber when growing under cultivation. The shadow prints (Figs. 1 and 2) annexed show the nature of this peculiarity. The lower pair of leaflets only is replaced by a pair of strongly developed pinnae, while the rest of the axis runs on singly pinnate and rather weak in structure. As a rule, no such continuation of the main axis is to be found.

In the case of *Liriodendron*, Jackson found some stages which could be regarded as progressive beyond the normal condition of the present species. Here the complexity was increased simply by augmentation of the number of lobes to the leaf.

This augmentation, as has often been shown, takes place in Acacias in the passage from the customary seedling leaf to the majority of bipinnate adults, a large number of pinnæ being added before the full-sized leaf is reached. But this mere addition of pinnæ scarcely seems to be the right interpretation of the increase in complexity if one compares the seedlings of *Liriodendron* and *Acacia*. What corresponds to the increase of lobes in the former is not so much the addition of pinnæ in



FIG. 1.—Seedling of *A. leprosa*, showing abnormal third leaf. (Natural size.)

the latter as the increase in degree of pinnation. Starting with a singly pinnate leaf, one arrives at a bipinnate form of remarkably fine structure in such species as *A. decurrens* Willd. But may there not exist a tendency toward triple pinnation in some of the forms? This question, suggesting itself, led to a rather careful search for evidence in its favor, with the result that in *A. decurrens* not a few leaves were discovered in which such a tendency was manifest. Of one of these leaves a shadow print is given (Fig. 3), showing clearly the third degree of pinnation on some of the basal leaflets of the pinnæ. How

much of a prophecy this is of a fully tripinnate leaf in certain Acacias of some future epoch no one can really tell; the tendency, however, cannot be without significance.

In his paper, which deals with animals as well as with plants, Jackson carries the same principle so far involved one step in advance in point of application. As a leaf develops base and tip first of all, he reasons that any change in shape which may add to its complexity will not appear at those points, but rather upon the proximal portions of the lamina. This he shows to be the case in *Liriodendron*, citing also several other examples in substantiation of his view.

In the case of the *A. leprosa* seedlings with abnormal development the lateral pinnæ may be regarded as further modifications of the proximal pair of leaflets of the ordinary first leaf of seedlings.¹ If this is, as seems probable, the right interpretation of such peculiar forms, it almost necessarily follows that the change in all the species at this stage is of the same nature, and that as a rule the higher, or more distal, leaflets upon the main axis lose the power to develop, on account of the greater strength of the newly developed lateral pinnæ. It may be worth while to state that these stages were found only after their prediction as the result of a course of reasoning, and were the direct objects of the search which led to their discovery.

The tendency toward triple pinnation is likewise, as may be easily seen by reference to the figure, only present upon the proximal leaflets of the pinnæ, and not at all to be found on the pinnæ near the tip of the leaf.

The final point to be discussed is the gradual metamorphosis to the phyllode. In seedlings where the change is gradual, as is the case in the great majority of species, but one pair of pinnæ is present at the time of its occurrence. In the abnormal seedlings shown, the prolongation of the axis is suppressed as the transition stages appear. In such cases it is possible to say with a high degree of certainty that the phyllode represents merely the flattened petiole. Next to be considered are the conditions of such forms as experience these changes later in life. *A. rubida* A. Cunn. and *A. heterophylla* Willd. have already been described by Reinke, and in his article one stage in the transition as it occurs in *A. heterophylla* is figured.



FIG. 2.— Abnormal seedling of *A. leprosa*.
(Natural size.)

¹ Cf. seedling of *Gleditsia*, where such transition stages are frequent.

According to that author the change is merely a gradual flattening of the petiole, accompanied by the reduction of parts more distal. The stage represented in his paper is explained in the following words: "Wo es zu breiten Phyllodien mit nur einem Fiederpaar an der Spitze kommt, entsprach in den von mir gesehenen Fällen das Phyllodium einem nur oberseits geflügelten Blattstiel, das Fiederpaar dem untersten Fiederpaar eines Fiederblattes, Spindel und höhere Fiederpaare würden somit als abortirt anzusehen sein. Steht auf der Spitze eines Phyllodiums einmal ein zweipaariges Fiederrudiment, so pfllegt die Spindel zwischen den beiden Fiederpaaren ungeflügelt zu bleiben" (p. 568).

Reinke is naturally giving only the results of his own observations, yet one cannot but draw the inference that a certain law is at least suspected, *viz.*, that only the petiole flattens in each case, and that at the same time the distal parts gradually cease to develop, until at last the stage is reached which this writer figures, after which the last pair of pinnæ fails to develop, and the phyllode is complete.

In the botanic garden of Harvard University there are two species of *Acacia* which show these transition stages in great abundance. They agree well in leaf characters with *A. rubida* and *A. heterophylla*, and will be discussed under these names, though full identification was not possible, owing to absence of flowers and fruit. Whether or not the determinations are right, the principle which they illustrate remains the same. Of both of these species the writer made a special examination during the spring of 1900, with a view to observing the different transition stages, their sequence and character. Upon re-reading Reinke's article in the summer of 1901, and finding there certain statements which in a way did not correspond with his results, he repeated the examination and ran across more peculiar forms which tend rather to disprove than to confirm the existence of any law governing such changes.

The first thing which appeared from these two examinations was that the method of reduction of the more distal parts described by Reinke, though indeed frequent, is perhaps not the most common of all. Rather more often an equal decrease

in size and final simultaneous disappearance of all the pairs of pinnæ was noted, as opposed to an unequal reduction starting



FIG. 3.—Leaf of *A. decurrens* showing tendency toward a triple pinnation.
(Slightly reduced.)

at the distal end. In this *A. rubida* seemed to be very regular; in *A. heterophylla* various methods of change were shown. As

far as sequence is concerned, there appeared to be no definite order, series of transition stages running in both directions.

There was also found a fairly large number of stages which lead one to doubt greatly whether in all cases it is the petiole only which is transformed to the phyllode, and whether, if one pair of pinnæ persists at a certain stage, that pair is always the proximal one. The prints which follow may, to be sure, represent mere anomalies, but from their number, at least, they cannot but raise in one's mind a certain amount of hesitation to

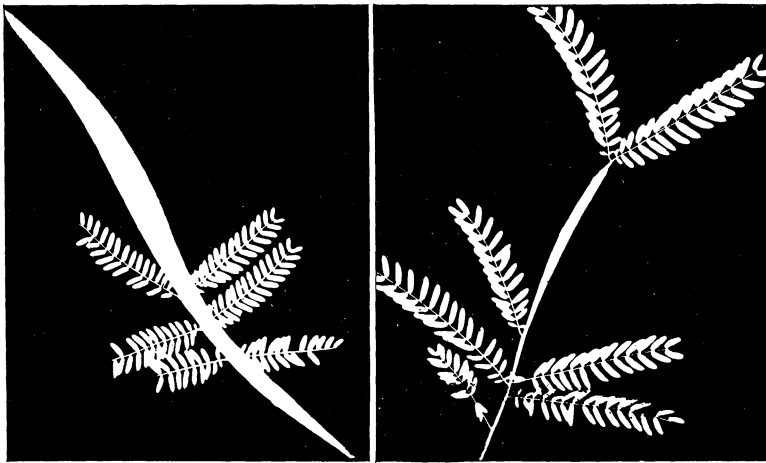


FIG. 4.

FIG. 5.

FIGS. 4 and 5. — *A. heterophylla*, variation in transition to phyllode. ($\frac{1}{4}$ natural size.)

consider the existence of a law as to method in any way established. Here the flattening appears in some cases entirely on the distal portions without affecting the petiole, in others both petiole and rachis are involved to varied extents. How these are to be interpreted under one definite law seems incomprehensible.

It is hardly to be expected, however, that the process of reduction of parts is going to follow the same strictly regular line as that of advancement. The two are brought about by entirely different causes and are in no way comparable. Therefore the fact that such changes as those last described occur does not greatly invalidate the testimony of the earlier presented

data in support of a principle dealing with a progression. On the whole, the conditions of the seedlings of *A. leprosa* and of the leaf of *A. decurrens* stand strongly in favor of the existence

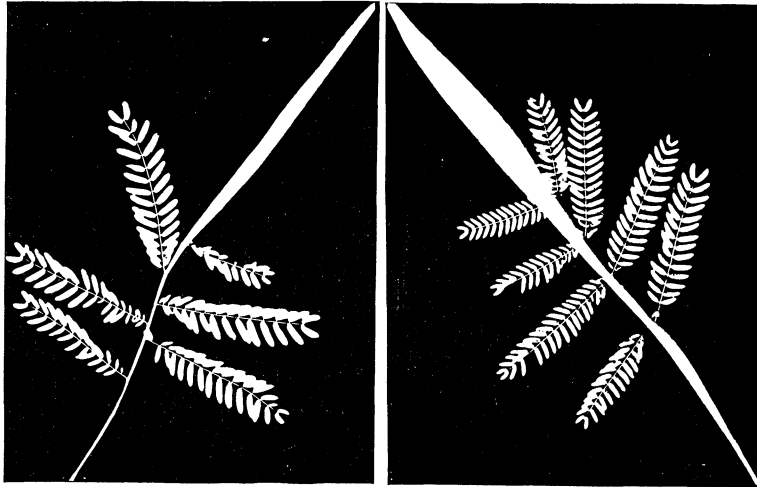


FIG. 6.

FIG. 7.



FIG. 8.

FIG. 9.

FIG. 10.

FIGS. 6-10. — *A. heterophylla*, variations in transition to phyllode. ($\frac{1}{4}$ natural size.)

of a regularly increasing complexity in leaf form, governed by fixed laws and repeated in an abbreviated form in plant ontogeny. To a certain extent also they add weight to Professor

Jackson's theory regarding stages in the development of a single leaf. The peculiar phyllode form rather discourages the idea of formulating any law covering phyllode formation, and lends an extremely potent meaning to Reinke's statement, "Der Wechsel von Phyllodien und Fiederblättern ist bei dieser Art [probably, as regards phylogeny, in others also] ein sehr mannigfaltiger."

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